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SYSTEMATICS AND ZOOGEOGRAPHY OF *THALAMOPORELLA GOTHICA* AND ITS ALLIED SPECIES (BRYOZOA, CHEILOSTOMATA)

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ABSTRACT

Thalamoporella gothica and its allied species are anascan cheilostome bryozoans which are distributed along subtidal, continental margins from the eastern Pacific, through the Atlantic and Indian Oceans, to the western Pacific. In the past, species within the *T. gothica* complex were thought to be only regional forms, and were treated as subspecies. However our examination of the group, and the consideration of newly collected material, has revealed at least five distinct species. While they are similar in general appearance, and share the same type of acutely shaped avicularium, they differ in a variety of other characters. The result is a new classification of this complex and a description of a new species from the Indian Ocean. The dispersal capabilities of *Thalamoporella* bryozoans are discussed and related to the distribution of the *T. gothica* complex. It is hypothesized that ancestral thalamoporellids were dispersed during the Tertiary through the Tethyan seaway and that they became isolated by subsequent tectonic events. The resulting speciation created the present complex which, while including the only two *Thalamoporella* taxa in the eastern Pacific, is not represented from the islands of the mid-Pacific.

When Don Abbott first spoke with two of us, John and Dorothy Soule, in late 1967, about contributing the section on Bryozoa for his planned volume on intertidal invertebrates, there was considerable consternation over the absence of published information on the life histories and zoogeography of the species which were ultimately included (Morris et al., 1980). Although Osburn (1950) had included locality data in his studies of eastern Pacific Bryozoa, his material was mostly collected from dredgings, meaning that coverage of shallow subtidal taxa was far from complete. In the Pacific Basin, bryozoan zoogeography was even more poorly known, except for data on the frequently collected, supposedly cosmopolitan, fouling species.

In the intervening years we have collected extensively throughout the Indo-Pacific, particularly in Polynesia, Melanesia, western Thailand and the Maldive Islands. From this work can be discerned distributional patterns which can be related to amphi-Atlantic and eastern Pacific species. Of added value have been studies of collections at the British Museum (Natural History) (BMNH) and specimens made available from the United States National Museum (USNM) and the American Museum of Natural History (AMNH).

The biology and zoogeography of one cheilostome family, Thalamoporellidae, and its principal genus, *Thalamoporella,* has been studied extensively by the present authors. For the first time, a relict Tethyan distribution can be hypothesized for a living bryozoan species (part of a complex of species) found in the eastern Pacific. *Thalamoporella gothica* and *T. californica* are closely related to Atlantic and western Indo-Pacific forms, in what we call the *T. gothica* complex, a complex that is entirely absent from the oceanic islands of the Pacific basin.

To demonstrate a distribution based on tectonic events, we have combined a systematic reevaluation of this complex, based on morphological characters specific to *Thalamoporella,* with a brief discussion of the group's probable dispersal capability supported by qualitative biological studies of *T. californica.*

MORPHOLOGICAL CHARACTERS

Recent collecting has shown that the Thalamoporellidae are common components of shallow subtidal faunas. Greatest species diversity is centered in the tropical Pacific. While primarily encrusting on hard substrates, algae and submerged wood, *Thalamoporella* colonies also develop into erect, cellariform, foliate or bilaminar forms. *T. californica* can grow off one substrate by forming jointed branches and then re-encrust on a new substrate (Hastings, 1930; Chaney, 1983), a habit not observed in other species of the genus.

The zooecia of *Thalamoporella* colonies are polymorphic, with four types divided between feeding autozooids and non-feeding heterozooids. Autozooids are distinguishable sexually with males being the most common. Female autozooids develop a large bilobate external ovicell, accommodating up to four embryos simultaneously (Fig. 1a, c).

Non-feeding heterozooids consist of kenozooids, formed as a result of localized shortages in space or a disturbance in colony structure (Powell and Cook, 1966), and avicularia, often large vicarious structures in which the zooecial opercula have enlarged into elongate mandibles (Fig. 1b, f). Avicularia are zooids modified by reduction or loss of their polypides and the expansion of the operculum and associated musculature. This enables them to perform defensive functions (Kaufmann, 1971; Winston, 1986) and in one species, *Bugula californica,* avicularia were observed to capture prey that was pulled apart by adjacent avicularia and ingested by the zooids (J. D. Soule et al., 1980).

Another morphological character of systematic importance is the calcareous spicules which develop interstitially in each zooid. In Bryozoa, these spicules are unique to the Thalamoporellidae and come in two forms, calipers (Figs. 1e, 7d, 8d) and compasses (Figs. 5e, 7d, 8d). Species of *Thalamoporella* can be separated on the basis of those containing either both spicule types or only one exclusively. In each case the spicules vary interspecifically in size and number. All known Recent *Thalamoporella* species have spicules. In contrast to past studies, it is now clear that spicule type is not necessarily species specific, and that systematic separations can only use these structures as one of a suite of morphological characters.

A third important morphological character is created by the two unequally sized bilateral opesiules which allow muscles to extend from the zooidal floor to the transparent frontal membrane (Fig. 1b). The opesiule walls flank the polypide tube and terminate unevenly either on the lateral walls or along the basal wall (Fig. 1d). The size, shape and number of these basal insertions is another systematic determinant that can be used to distinguish species within a given complex. The opesia, or opening in the primitive calcified frontal wall (cryptocyst) consists of the apertural area only, in contrast to forms such as *Membranipora* which have an entirely soft frontal.

Avicularian Characters

Avicularian morphology has long been recognized as of primary taxonomic importance in the study of thalamoporellids (Levinsen, 1909; Harmer, 1926; J. D. Soule and D. F. Soule, 1970; D. F. Soule et al., 1987). The study of this structure is considered to be the single most reliable character and can be used to separate the *Thalamoporella* into a series of lineages or complexes each of which have widespread distributions.

Although there are species where no avicularia occur (D. F. Soule and J. D. Soule, 1964), these are regarded as exceptional among Recent forms. Avicularia

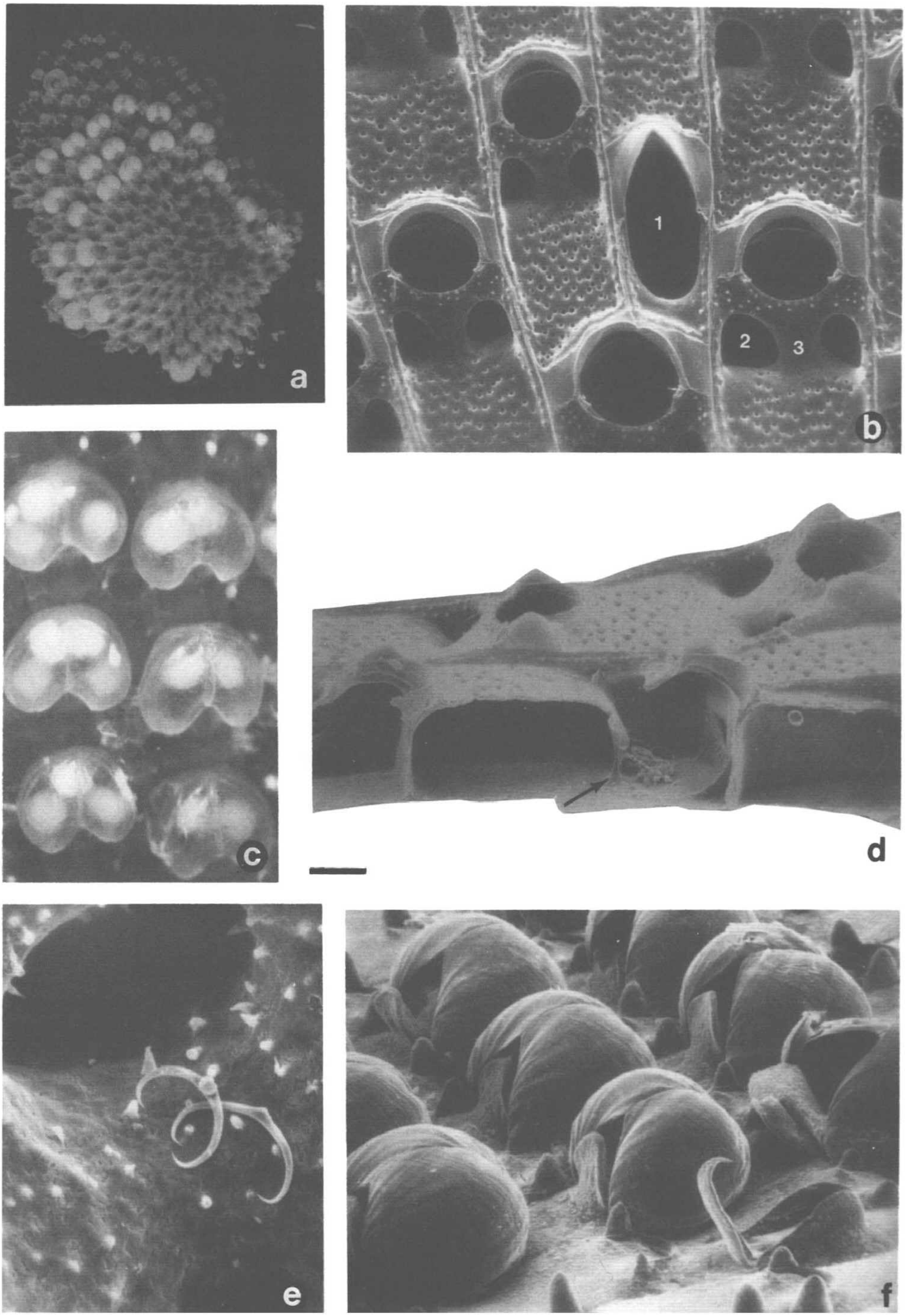

Figure 1. Morphological structures of *Thalamoporella.* a, small encrusting colony of *T. californica,* showing arrangement of ovicells (Scale bar = 1 mm). b, *T. floridana* after cleaning, avicularium (1) is adjacent to its "sibling" autozooid (left), both bud from the same distal end of an autozooid (below); each autozooid has two unequal opesiules (2) and a smooth cryptocyst (3) over the polypide tube (Scale = 100 μm). c, *T. californica* with two rows of female autozooids that have ovicells bearing up

in fossil *Thalamoporella* are quite common, and where they are lacking in a given specimen it may be more indicative of inadequate sampling than biological reality. Fossil avicularia tend to be larger than Recent counterparts which suggests that they once had functional polypides (D. F. Soule et al., 1987). The vast majority of Recent species which do possess avicularia can be divided into various lineages based on their gross morphology. A basic subdivision occurs between species which have a rounded mandible and those where the mandible is acute. This difference is reflected by the skeletal features of the rostrum which forms the distal portion of the avicularium beyond the articulation of the mandible (Fig. 2).

Further discussion of the differences between each of these structures is beyond the scope of the present work (Soule et al., in prep.). In the case of the *T. gothica* complex, the distal end of the rostrum is arch-shaped, with a round, thinly calcified lucidum or "window," proximal to the tip of the arch. The lineage of species groups with acute avicularia most similar to *T. gothica* is represented by *T. stapifera* (Fig. 2c), an Indo-Pacific species whose range extends to Hawaii. Comparison of the stapiferan avicularium with that of *T. gothica* (Figs. 2c, 5d) shows basic differences in the rostral shape and the presence of a beaded mural rim around the proximal opesia.

DISPERSAL IN THALAMOPORELLA

Mechanisms of dispersal for encrusting cheilostome bryozoans which do not produce planktotrophic larvae are restricted either to asexual growth as colonies along subtidal substrates or to sexually produced swimming larvae which colonize new substrates. An added benefit of larval settlement occurs when species attach to portable substrates, such as floating kelp, logs, or pumice, and then reproduce sexually before these surfaces are degraded. Unlike other lecithotrophic bryozoans which have attained cosmopolitan distributions by fouling ship hulls, the Thalamoporellidae have not generally utilized fouling as a form of transport.

Asexual colonial growth by astogeny can account for a long term lateral dispersal along shallow water margins, assuming the availability of substrates. Again, dispersal is enhanced when algal substrates are dislodged and transported, as with the rafts of kelp commonly seen in the temperate eastern Pacific.

The most efficient mode of dispersal is by sexual reproduction. The female autozooid can produce a number of embryos which mature in the ovicell and then are released as swimming coronate larvae. The intensity and duration of sexual reproduction varies seasonally, but has been observed to occur continually in *T. californica* along southern California (Chaney, 1983). The formation of ovicells has not been reported in three of the species discussed below, *T. floridana, T. indica* and *T. spinosa*. This may indicate a very low level of sexual reproduction in favor of colonial growth by asexual budding. There is no evidence of endozooecial (internal) ovicells and it is unlikely that two different reproductive structures should exist in the genus.

The end result of sexual reproduction is the release of meroplanktonic swimming larvae, their subsequent settlement and establishment of new colonies. As *Thalamoporella* larvae are lecithotrophic, their swimming activity is limited to a few

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to four embryos (Scale = 200 μm). d, side view of *T. indica* with right lateral wall removed from an autozooid showing insertion of opesiule wall (arrow) on basal wall (Scale = 100 μm). e, caliper spicules near opesiule of *T. spinosa* (Scale = 10 μm). f, side surface view of *T. californica* colony with ovicells and avicularium (lower right) with its open mandible (Scale = 200 μm).

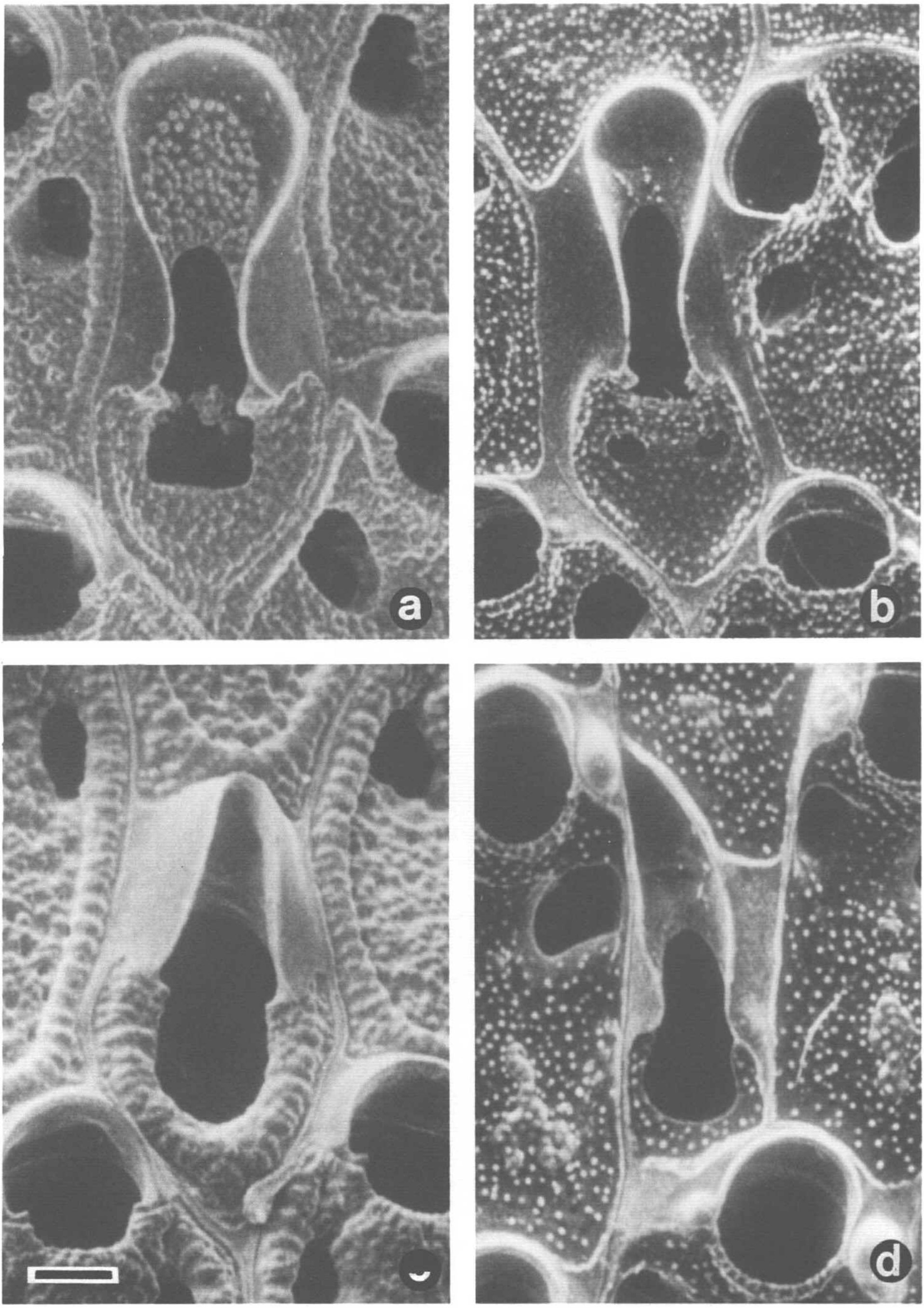


Figure 2. Types of avicularia in *Thalamoporella*. a, rounded rostrum with large proximal opesia. b, rounded rostrum, with two proximal opesiules (*T. distorta*). c, widely acute rostrum with a beaded mural rim (*T. stapifera*). d, acute rostrum which is torqued to one side (*T. falcifera*). Scale for all figures = 100 μm.

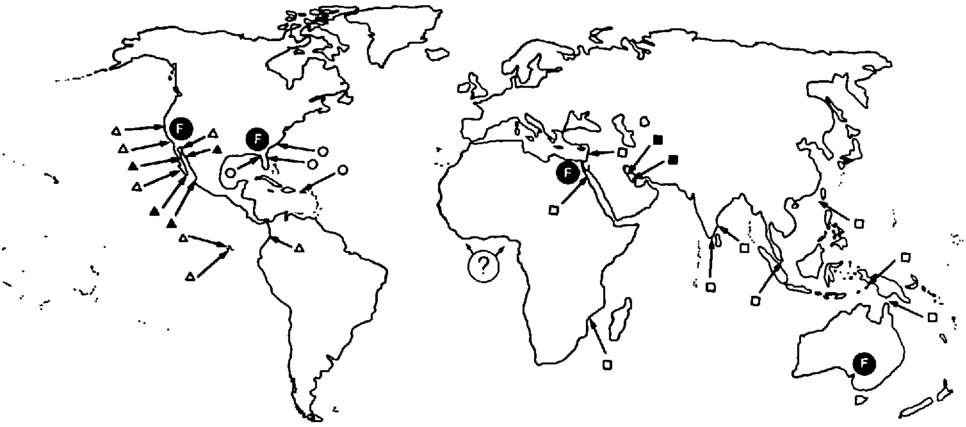


Figure 3. The distribution of the *T. gothica* species complex along continental margins from the eastern Pacific to the western Pacific, following a Tethyan track. Symbols: *T. californica,* white triangles; *T. gothica,* black triangles; *T. floridana,* circles; *T. indica,* white squares; *T. spinosa,* black squares. Possible new taxon, "?" (see text). Known Tertiary deposits of *Thalamoporella* also indicated (F).

hours. For example, periods of successful settlement and metamorphosis in *T. californica* larvae are limited to the first 10–12 h after release (Chaney, 1983).

These aspects of *Thalamoporella* life history are limiting factors to their global dispersal capabilities. Our collecting evidence supports the view that modern biogeographic features, such as the Eastern Pacific Barrier (Ekman, 1953; Vermeij, 1978), have effectively blocked any transport between the Indo-Pacific and the eastern Pacific. The Indo-Pacific Province is populated by numerous species found in reef rubble that represent all of the species lineages within the Thalamoporellidae.

However in the case of one such grouping, the *T. gothica* complex, this representation is restricted in distribution and no *gothica*-type forms having been found around the tropical mid-Pacific islands. Instead the distribution of this complex extends from continental margins of the tropical and subtropical western Pacific, across the Indian Ocean and the Atlantic, through the Caribbean and along the coastline of the eastern Pacific (Fig. 3). The only two species of *Thalamoporella* found in the eastern Pacific are both members of this group, suggesting a dispersal path from the Atlantic through the Gulf of Mexico and subsequent speciation when they became geographically isolated by closure of the Panamanian isthmus.

SYSTEMATICS

The genus *Thalamoporella,* characterized by individual zooids with bilateral frontal muscle insertions which give it the appearance of a vase with two handles on the neck, was described by Hincks (1887). Unfortunately, he designated the type as *Flustra rozieri,* a species known only from an illustration by Savigny (1817?) and named by Audouin (1826) with no further description. This illustration showed prominent ovicells but no avicularia. The type species came either from the eastern Mediterranean or the Red Sea. As part of our monographic survey of the Thalamoporellidae (in prep.), a neotype for *T. rozieri* is being designated to ameliorate this problem.

Thalamoporella gothica Species Complex

Membranipora gothica Busk, 1856 was described from Mazatlan, west Mexico and placed in *Thalamoporella* by Levinsen (1909) as a subspecies, *T. rozieri* var. D (*gothica*) in keeping with the description of Hincks (1880) of *Steganoporella rozieri* form *gothica.* Since that time the literature has become greatly confused by the ambiguous use of *T. rozieri* for species or subspecies with either acute or rounded mandibles (see D. F. Soule et al., 1987 for further discussion). Levinsen (1909) also described *T. rozieri* var. *californica,* which is superficially similar to *T. gothica,* and may have in fact been included in Busk's type material from which Harmer selected the lectotype.

Since *T. gothica* was given species status by Harmer (1926), it has been cited, sometimes with its own subspecies, by various authors for specimens from California, the Caribbean, Africa, Indian Ocean, and the western Pacific, while *T. californica* was given species status by Hastings (1930). *T. gothica* var. *floridana* Osburn, 1940, was raised to species level by Winston (1982). *Steganoporella rozieri* var. *indica* Hincks, 1880, was placed in *T. gothica* var. *indica* by Harmer (1926), who also included in that variety *T. rozieri* var. *labiata* Levinsen, 1909 and other material from India, Ceylon, Formosa Strait, Torres Strait and Australia. It is now possible to distinguish several species, all with superficial similarities to *T. gothica,* but with sufficient differences to allow separate morphological characterizations and a revised view of their zoogeographic distributions.

It is not possible to determine the ancestral species of this complex, but the genus is known from the Eocene of Egypt (Ziko, 1985) and Florida (Cheetham, 1963). Diversity in zooecial form and avicularian structure of *Thalamoporella* has been found in fossil deposits in the Caribbean which date from the lower Miocene (Canu and Bassler, 1919; 1920) and in Australia from the Pliocene (Maplestone, 1900; Canu and Bassler, 1935). At this time we have been able to recognize six different morphs attributed to this complex, of which five are considered to be sufficiently characterized to warrant species status. There is insufficient material of the other to make a determination. Each will be outlined in the following classification.

CLASSIFICATION

Family THALAMOPORELLIDAE Levinsen, 1902
Genus *Thalamoporella* Hincks, 1887

Diagnosis.—Autozooids with porous cryptocysts, perforated by bilateral, asymmetrically rounded opesiules, proximal to aperture, flanking the polypide tube, and connecting to basal or lateral walls. Avicularia vicarious, rostrum either rounded or acute. Internal calcareous spicules occur in the form of compasses and/or calipers. Hyperstomial ovicells bilobate and prominent. Colonies erect, branching, or encrusting.

Thalamoporella gothica (Busk), 1856
Figures 4c–e

Membranipora gothica Busk, 1856
Steganoporella rozieri form *gothica*: Hincks, 1880
Thalamoporella rozieri var. *D.* (*gothica*): Levinsen, 1909
Thalamoporella gothica: Harmer, 1926

Description.—Autozooids large for genus, 0.70–0.90 mm in length, with a rhomboidal aperture measuring wider than high and having a thin rim. Adoral tubercles reduced to tiny mounds or absent. Frontal granular with small pores; granular portion of the frontal not depressed over the polypide tube. Opesiules plain. Single basal insertion open distally, either as a rod or an L-shape, but not hooked (Fig. 4c). Avicularia ovoid, tapering distally to a subacute point of a gothic arch (Fig. 4d). Avicularian opesia large, and the proximal cryptocyst very narrow. When lit obliquely distal rostral shelf (palate) shows a large lucidum. Each lateral wall with four interzooecial pore plates. Both types of spicules are present. Length of calipers range from 40–100 μm, while compasses are the longest in the complex, measuring from 75 to 480 μm (Fig. 5). Ovicells have been observed, but are not as numerous as in *T. californica* (Fig. 1f). Colonies encrust substrate.

Material Examined.—Lectotype: BMNH 99.7.1.1511; Mexico: Isla Tiburon and Mazatlan (Soule Coll.); Cabo San Lucas and Bahia de Los Angeles, Baja California (Chaney Coll.); Gulf of California (Allan Hancock Foundation Coll: AHF).

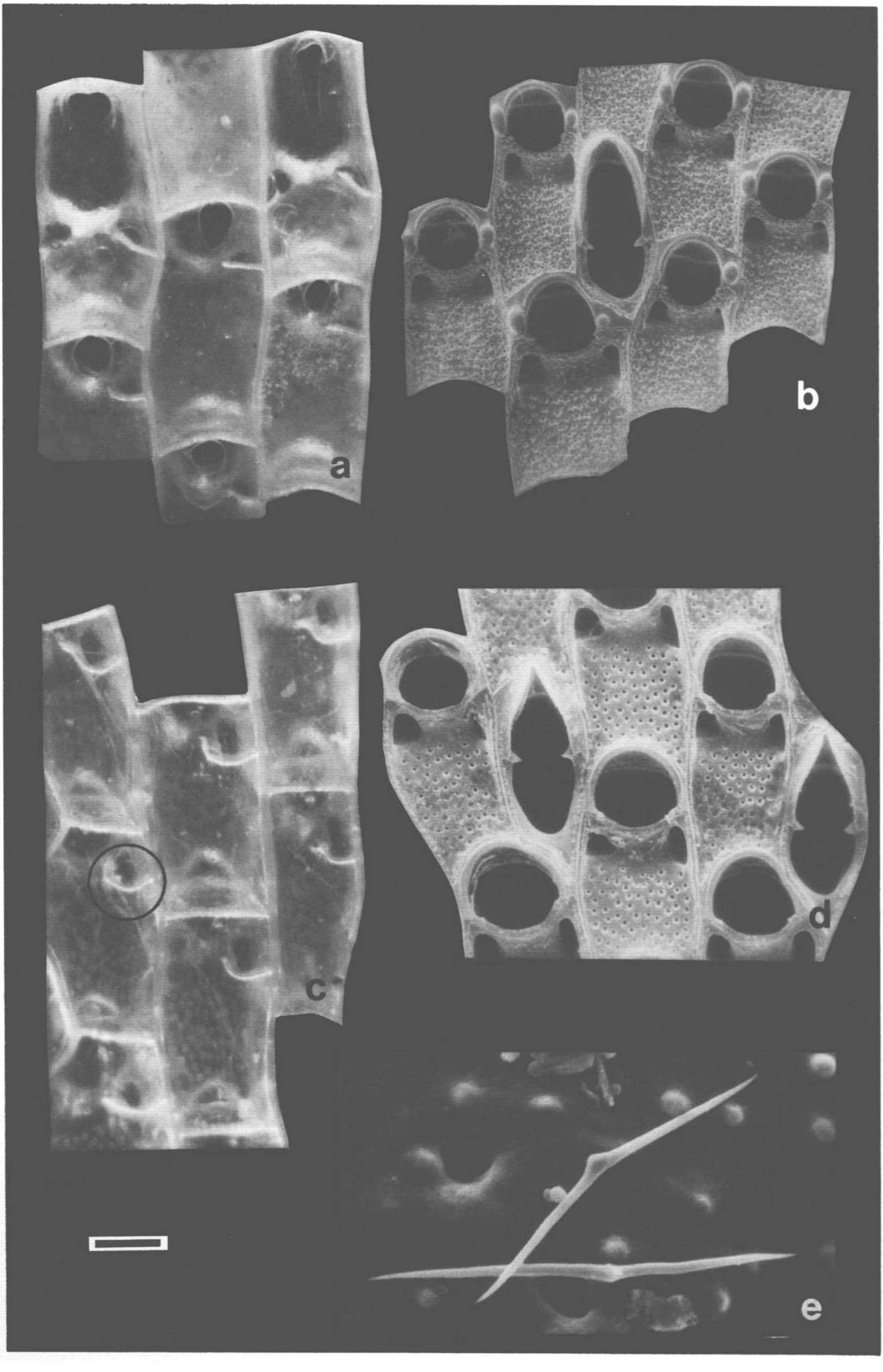
Distribution.—Throughout the Gulf of California from Cabo San Lucas, Baja California Sur to Mazatlan, Sinaloa, west Mexico, the type locality (Fig. 3). From the intertidal to a depth of 10 m, in rubble.

Discussion.—*T. gothica* (s. s.) is most readily confused with *T. californica* since they co-exist in the Gulf of California. Citations of specimens occurring in southern California are apparently in error. Each of these specimens so labeled (AHF and BMNH) has been a misidentified *T. californica. T. gothica* can be separated from *T. californica* by comparing the shape of the avicularia, the zooecial aperture and, most importantly, by noting the presence of both types of spicules. The erect, cellariform growth form of *T. californica* is also distinctive. Apart from *T. californica,* it differs from all other nominate species in the complex by having one open basal insertion and four lateral pore plates. It is ironic that the species whose name has been widely used to identify *Thalamoporella* from many regions of the world does in fact have a very limited distribution in the eastern Pacific, especially in relation to *T. californica.* The size of autozooids of *T. gothica* within a single colony are often quite variable, particularly their width, indicating a high sensitivity to substrate configuration and environmental conditions during growth.

Thalamoporella californica (Levinsen, 1909)
Figure 4a–b

Steganoporella rozieri form *gothica* Hincks, 1880 (part)
Thalamoporella rozieri: Robertson, 1908
Thalamoporella rozieri var. E (*californica*) Levinsen, 1909
Thalamoporella californica: Hastings, 1930

Description.—Autozooids smaller than in *T. gothica,* measuring 0.50–0.65 mm in length with a subtriangular aperture higher than wide (Fig. 4b). Adoral tubercles usually present, often tall and thin, very conspicuous in some populations while absent in others. Frontal not depressed over polypide tube, with plain unadorned opesiules, unequally sized. Single basal insertion either a straight line or narrow buttonhook, sometimes absent on the basal wall or accompanied by a second, tiny bar from the adjacent lateral wall (Fig. 4a). Avicularia large and ovoid, about 85% as long as autozooids, widest mediodistally, tapering to a rounded point ("gothic" arch). Distal rostral rim may extend over the proximal margin of the next zooid, may contain a small lucidum. Proximal cryptocyst narrow with a large opesia. Four pore plates on each lateral wall. Spicules calipers only, from 40–180 μm in length, very numerous (Fig. 5). Ovicells conspicuous in most populations observed. Colonies either encrust or form dichotomous cellariform branches with distinctive chitinous joints.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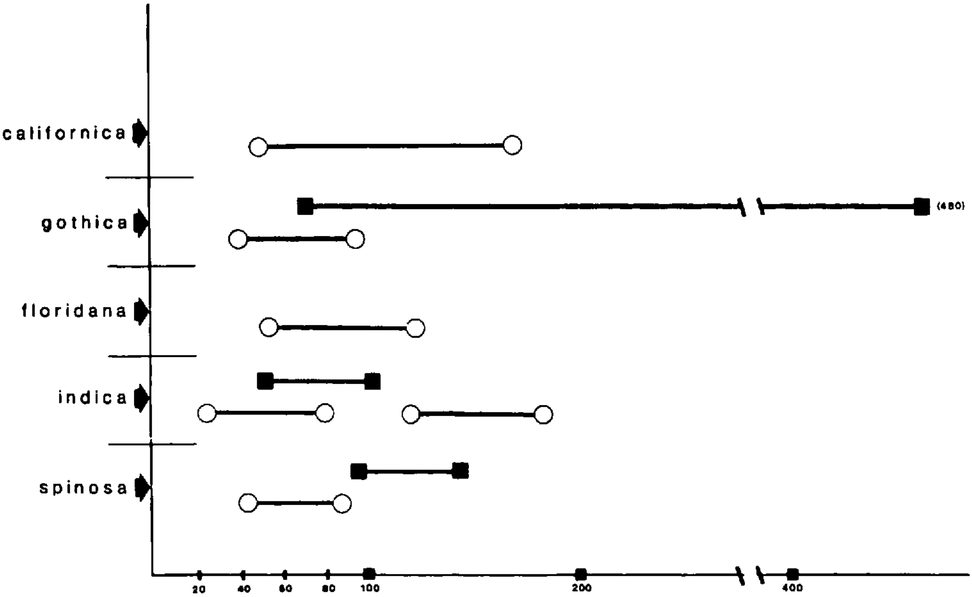

Figure 5. Comparative ranges in spicule lengths for the *T. gothica* species complex. Calipers (circles) and compasses (squares) are paired by taxa, two species have calipers only.

Material Examined.—Holotype: BMNH 28.9.13.52, Santa Monica Bay, California (Hincks Coll.); California: Monterey Bay and Santa Catalina Island (Chaney Coll.); Channel Islands (AHF Coll.); Pleistocene deposit, Newport Mesa, Orange Co. (Los Angeles County Museum of Natural History, Sta. 66-2); Mexico: Puerto Penasco, Sonora (Soule Coll.); Bahia Tortugas, Baja California Sur (Chaney Coll.); Galapagos Islands: James Bay and Tagus Cove (BMNH Coll.); Colombia: Isla Gorgona (AHF Coll.).

Distribution. — *T. californica,* occurs from Monterey Bay, central California to Isla Gorgona, Colombia (Abbott, 1987; Osburn, 1950). The type locality is Santa Monica Bay, California (Fig. 3). Common on algal substrates from low intertidal to about 15 m. Often found in the holdfasts of *Macrocystis* (see section on dispersal, above). Hastings (1930) examined specimens dredged in 15 fm from the Galapagos. Colonies have been collected from Pleistocene deposits in Southern California (Soule and Duff, 1957).

Discussion.—The similarities between *T. californica* and *T. gothica* have been discussed above. *T. californica* differs from *T. floridana,* its probable Atlantic cognate, by having a much larger avicularium, open basal insertions, and four lateral pore plates.

A second form from the Atlantic has been noted by Cook (1964) as *T. gothica* and has been collected from Senegal to Ghana, West Africa (see Fig. 3; marked "?"). It bears a general resemblance to *T. californica* but differs in having both types of spicules, smaller avicularia and a pronounced, wide sinus in the auto-

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Figure 4. The *Thalamoporella* from the eastern Pacific. a, obverse view of *T. californica* showing simple basal insertion. b, top view of same. c, obverse of *T. gothica* with curved basal insertion (circled). d, top view of same with the distinctive gothic arch of the avicularium. (Scale bar, Figs. a–d = 200 μm.) e, small compass spicules of *T. gothica* (Scale = 10 μm).

zooidal aperture. Polypide tentacles numbered 14–15 in this form (Cook, 1964), while *T. californica* has 21 tentacles in male autozooids and 15–18 in females (Chaney, 1983). Correct disposition of this form is awaiting further detailed examination.

Thalamoporella floridana (Osburn), 1940
Figure 6a, b

Thalamoporella gothica var. *floridana* Osburn, 1940
Thalamoporella floridana: Winston, 1982

Description.—Autozooids 0.50–0.65 mm in length, with a nearly circular aperture that may be proximally arcuate in some specimens. Adoral area may have small tubercles. Cryptocyst over the polypide tube depressed between variably sized, plain opesiules (Fig. 6b). Single basal insertion finger shaped and closed to the lateral wall (Fig. 6a). Avicularium about 65% of the length of an autozooid, with widely arcuate opesia, rounded rostral chamber, and mandible shaped as an equilateral triangle without developed hinges mid-laterally. Two pore plates on each lateral wall. Spicules consist of calipers only, 30–120 μm in length (Fig. 5). No ovicells reported or figured. Colonies either encrust or form foliaceous bilaminar clumps which can act as settlement substrates for other invertebrates.

Material Examined.—South Carolina: (Soule Coll., no specific locality); Florida: Fort Pierce and Appalachicola (AMNH Coll., not numbered); Florida (AHF, Osburn Coll.).

Distribution.—*T. floridana* has been collected from North Carolina (Maturo, 1957) to western Florida. It is found in the Caribbean at least as far south as Guanica Harbor, Puerto Rico (type locality). It probably occurs throughout the Caribbean Basin and the Gulf of Mexico and is seasonally common intertidally and in shallow depths (Fig. 3).

Discussion.—*T. floridana* is similar in gross morphology to *T. indica* but differs in the configuration of the basal insertion. It also differs by having only caliper spicules.

The occurrence of "a few spicules in the form of open compasses" in a *T. floridana* specimen was earlier reported without elaboration by Maturo (1957) from Beaufort, North Carolina. We have observed in other species that caliper spicules sometimes do not form completely, thereby appearing to be small compasses under low magnification.

Thalamoporella indica (Hincks), 1880
Figure 6c, d

Steganoporella rozieri var. *indica* Hincks, 1880
Membranipora gothica var. *indica* Hincks, 1880
Thalamoporella rozieri var. A. (*labiata*) Levinsen, 1909 (part)
Thalamoporella gothica var. *indica*: Harmer, 1926 (part)

Description.—Autozooids 0.45–0.65 mm in length, having a circular aperture with a wide sinus. Adoral tubercles, when present, small. Cryptocyst over the polypide tube depressed, usually smooth with little surface granulation or pores. Opesiules small, unequally sized, unadorned (Fig. 6d) or with minute spinules. Single basal insertion a closed finger-shaped loop (Fig. 6c). Avicularium about 65% the length of an autozooid, opesia wide, rounded, rostrum arched, raised. Two pore plates on each lateral wall. Both types of spicules present; compasses 50–100 μm, calipers

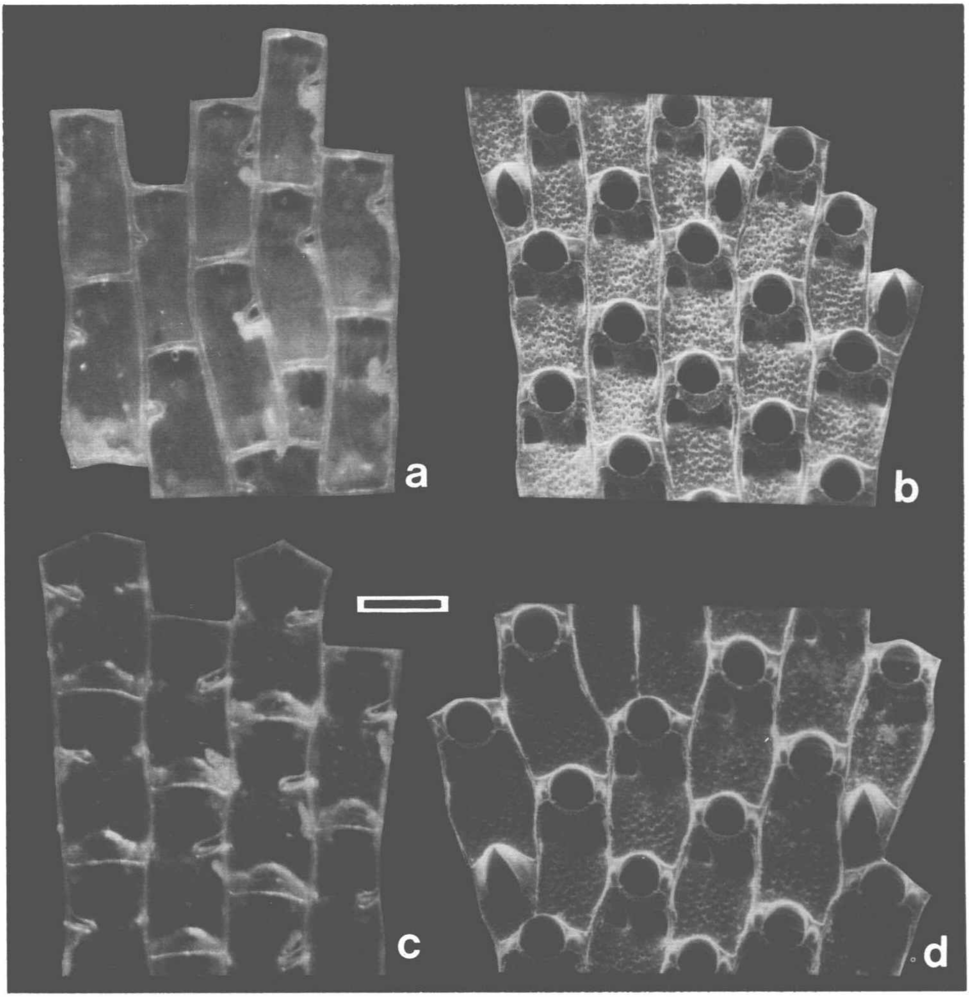

Figure 6. *Thalamoporella* from the west Atlantic and Red Sea. a, obverse of *T. floridana* showing a closed loop basal insertion. b, top view of same. c, obverse of *T. indica* with similar basal insertion. d, top view of same (Scale bar, all figs. = 200 μm.)

in two distinct size classes, 20–80 μm and 130–180 μm (Fig. 5). Hincks figured an ovicell in the original description, but no examples were observed in material examined. Ovicells have also been reported by Okada and Mawatari (1935). Colonies occur as erect, bilaminar, and foliaceous.

Material Examined.—Lebanon: Beirut, collected by J. G. Harmelin (Soule Coll.); Red Sea: BMNH, no number (Hincks Coll.); Mozambique: BMNH 1986.7.28.16, 5 km north of Courengo Marques; Bahrain: BMNH 28.4.4.1, buoy (not figured); India: BMNH 91.4.30.10, Madras; BMNH 28.9.13.56, Pamban (as Paumben) Island, Tamil Nadu, collected by E. C. Jelly, 24 October 1898 (Cambridge Museum Coll.); Singapore: BMNH 28.9.13.53, New Harbor, det. by G. M. R. Levinsen, *Siboga* Expedition; Taiwan: BMNH 28.9.13.57 as whole mount, Formosa Strait, collected by Levinsen, 11 September 1900, as type of *T. rozieri* var. A *labiata*; Indonesia: BMNH 28.3.6.112 as whole mount, Jedan, Aru Islands, *Siboga*; Australia: BMNH 28.9.13.54 Torres Straits, det. by Levinsen, 6 February 1902, *Siboga.*

Distribution.—*T. indica* occurs in the eastern Mediterranean, along East Africa to Mozambique, east to the Torres Strait and the South China Sea (Fig. 3). Records from Japan (Okada and Mawatari, 1935) are not shown in Figure 3 because the material was not examined. The type locality is "from India." The species is believed to have repopulated the eastern Mediterranean by migrating through the Suez Canal during the past century as salinity barriers became reduced (see Powell, 1969 for discussion and figure).

Discussion.—Apart from differences in spicule type, *T. indica* is closest to *T. floridana* in all other characters, including its growth form as foliaceous masses. *T. indica* differs from *T. spinosa* by the shape and larger size of its autozooidal aperture. Most specimens examined lacked opesiule spinules, a character consistently present in *T. spinosa.*

By amending Hincks' original description, Harmer (1926) constructed *T. gothica* var. *indica* and synonymized Levinsen's *T. rozieri* var. A. *labiata.* This latter form was personally collected by Levinsen from the Formosa Strait. In his view, the decisive taxonomic character was a subtriangular aperture, bordered by a distinct, heavily ridged proximal lip. However, the occurrence of this character is inconsistent, even between autozooids of Levinsen's type specimen (BMNH 28.9.13.57) and is regarded here as a transitory character, possibly environmentally stimulated.

Thalamoporella spinosa new species
Figure 7

Thalamoporella rozieri var. *labiata* Levinsen, 1909 (part)
Thalamoporella gothica var. *indica* Harmer, 1926 (part)
Thalamoporella gothica: J. D. Soule, 1985

Diagnosis and Description.—Autozooids rectangular, 0.36–0.47 μm in length, with subtriangular or hoof-shaped apertures; proximal lip straight, beaded, ridged; very large adoral tubercles (Fig. 7a). Frontal cryptocyst short, with fine granules around pores, and small irregular curved spinules on frontal around opesiules (Fig. 7e). Cryptocyst depressed over the polypide tube and skewed toward smaller opesiule (Fig. 7c). Opesiules unequal in size. Larger opesiule descends to basal wall forming a single narrow loop closed against the lateral wall (Fig. 7b). Avicularium about 80% the length of autozooids, with rounded base, raised distal rostrum, mandible acute. Avicularian opesia large with proximal cryptocyst narrow, distal cryptocyst (palate) beneath mandible a curved shelf and the central area (lucidum) thin (Fig. 7c). Two lateral pore plates present. Both type of spicules present (Fig. 7d). Calipers wider than high, width 40–90 μm; compasses wide open, length 90–155 μm (Fig. 5). Ovicells unknown. Colonies encrust algae.

Holotype Number.—AHF 188.

Type Locality.—Manifa, Saudi Arabia (27°39'67"N, 49°01'30"E), Station 1G2 of the Northern Area Benthic Study (NABS), collected 3 April 1985, on sea grasses near coral reef in 3 m.

Material Examined.—Saudi Arabia: 12 NABS stations along Persian (Arabian) Gulf coast, on sea grass (see J. D. Soule and D. F. Soule, 1985 for station details), all specimens currently in Soule Collection; United Arab Emirates: BMNH 1965.5.1.4.9, Khot al Bazaini.

Distribution.—Presently restricted to the Persian Gulf (Fig. 3).

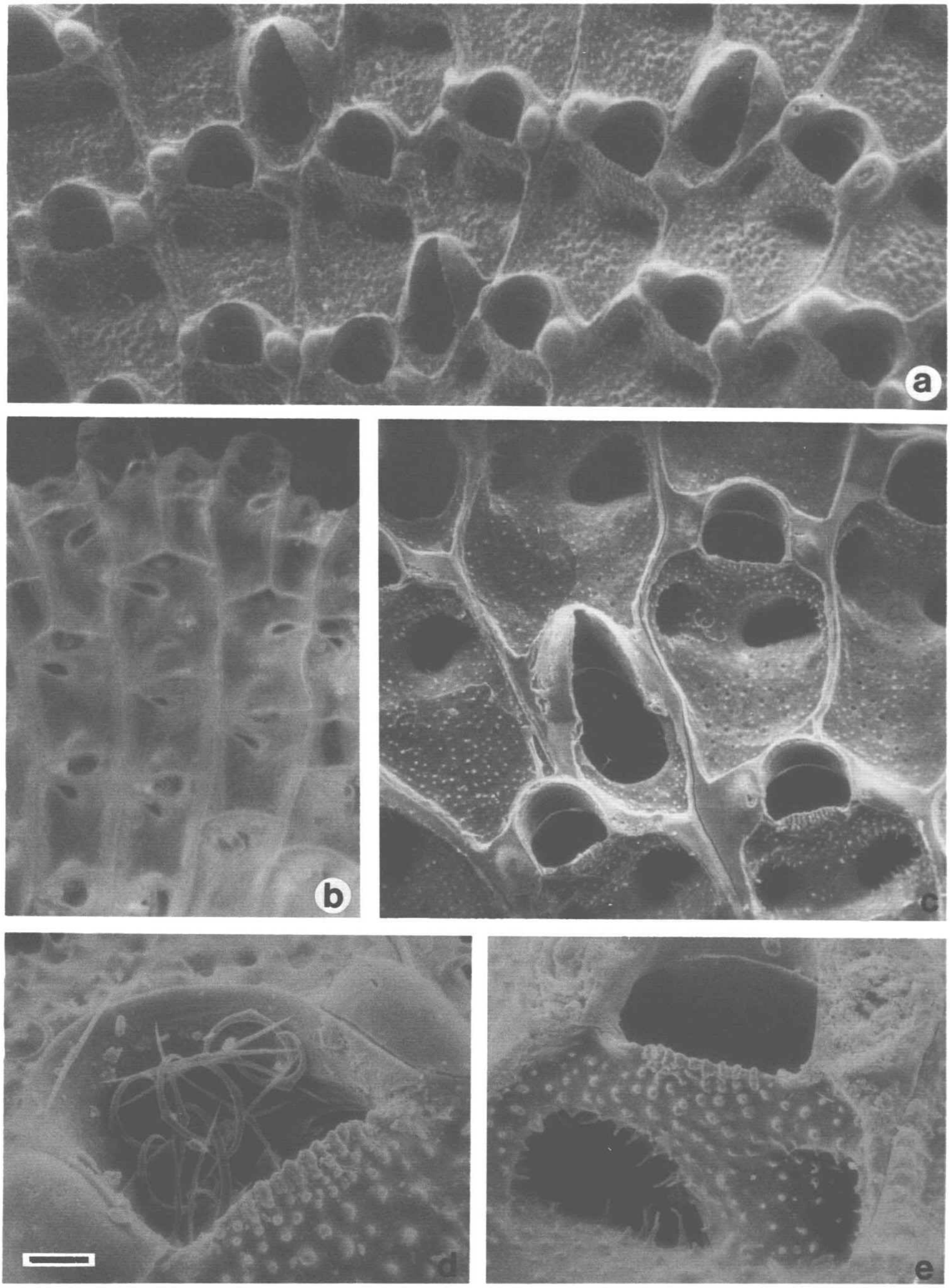

Figure 7. *Thalamoporella spinosa* n. sp., views of the holotype. a, top view of the colony, with adoral tubercles of various dimensions (Scale bar = 100 μm). b, obverse view of basal insertions showing prominent, single closed loops (Scale = 150 μm). c, detail of avicularium and autozooids (Scale = 75 μm). d, a collection of spicules in zooecial aperture after cleaning, note granulated proximal lip (Scale = 20 μm). e, detail of opesiule showing irregular spinules, a unique character. Cryptocyst is very depressed over the polypide tube (Scale = 30 μm).

Discussion.—This form has previously been included in *T. gothica indica* by Harmer (1926) who placed in synonymy such varied forms as *T. rozieri* var. *labiata* Levinsen, 1909 with a wide straight or protruding proximal lip, *T. gothica* var. *indica* with an arcuate, sinusoid narrow proximal lip and lacking frontal spines and *T. spinosa,* with a straight, ridged proximal lip and frontal spinules. Soule and Soule (1985) followed Harmer's precedent in identifying material from the Saudia Arabian coast of the Persian Gulf, but the acquisition of additional specimens from that region, coupled with the examination of Hincks', Levinsen's and Harmer's material at the British Museum has led us to distinguish *T. spinosa* from variations of *T. indica.* Both species co-occur in the Persian Gulf. Apart from *T. indica,* the new species differs from all others in the complex by the presence of conspicuous spinules around the zooecial opesiules.

It differs from *T. indica* in having a smaller, hoof-shaped aperture, larger avicularia, and in lacking large caliper spicules. The growth form also appears distinctive. *T. spinosa* encrusts algae and sea grasses while *T. indica* grows in erect, bilaminar, foliose masses.

Superficially, *T. spinosa* also resembles specimens of an undescribed species *Thairopora* collected from the Red Sea on algae (BMNH 1897.5.1.595, ex Lunt Coll.) but the avicularia of *T. spinosa* lack a biperforated cryptocyst. While long recognized as the second genus of Thalamoporellidae, the morphology, distribution and specific relationships in *Thairopora* are poorly understood. (Manuscript submitted for publication.)

BIOGEOGRAPHIC PERSPECTIVES

The present distribution of these closely related species of *Thalamoporella* seems consistent with those of other invertebrate taxa that dispersed along the Tethyan seaway of the early Tertiary. The distribution of marine invertebrates by way of the Tethys has been explored by numerous workers and will not now be extensively recounted (Adams, 1967; Valentine, 1973; Hallam, 1981). In many cases studies of this phenomena have been strictly paleontological, using taxa present only in the Tertiary fossil record without any emphasis on Recent species. Biogeographic studies using Recent Bryozoa taxa have been broad-based, often characterizing various faunal provinces by diversity indices as opposed to studying particular genera (see Schopf, 1976 for review). Exceptions are reports on the Tethyan biogeography of Bryozoa which use paleontological evidence that relates to present Indo-Pacific forms (Pouyet and David, 1979; Braga, 1987). Documentation of a westward migration of Bryozoa from the Tethys to the Western Hemisphere has not been illustrated with records of Recent species, apart from studies which, by emphasizing the cosmopolitan nature of a particular taxon, may have obscured its systematic heterogeneity (Harmer, 1926; Osburn, 1950).

Despite the limited dispersal capabilities of *Thalamoporella,* transport across the Atlantic during the Tertiary was probably not unusual. A westward flowing current through the Tethys, analogous to the present North Equatorial Current, could have propelled colonies on floating debris or algae at a velocity of several knots. Since the Atlantic of the late Cretaceous and early Tertiary was narrower than present day, passively drifting forms could have completed a crossing in as little as 4 to 6 weeks, less than half the time presently possible (Scheltema, 1971; 1976). Although success in recolonization would depend on a number of environmental factors, the great length of time available for this process would ensure that an ancestral *gothica* species had probably dispersed along the tropical margins of two-thirds of the globe during the existence of the Tethyan seaway.

There is without question a dearth of fossil evidence. Apart from the Pleistocene record of *T. californica* (Soule and Duff, 1957), there have been no fossil specimens of this complex reported, a fact probably more attributable to a lack of collecting. Since one *Thalamoporella* species, *T. ocalana* Cheetham, 1963, has been found in Eocene deposits in Florida, we could assume that a *gothica* ancestor was also present during that era. Its center of origin can only be inferred from examples given in studies of Tethyan biogeography which postulate species radiations along that shallow seaway.

Speciation into the present five or six nominate taxa was undoubtedly punctuated by a series of tectonic events, commencing with the close of the eastern Tethys (completed in the Miocene), which isolated the Indian Ocean populations that would diverge into *T. indica* and *T. spinosa.* The closure and desiccation of the Mediterranean during the Miocene removed marine forms until they could be reintroduced by migration of Atlantic taxa through the Strait of Gibraltar. Up to the present day, this recolonization has apparently not included Atlantic *Thalamoporella,* represented by *T. floridana* and the form from west Africa. A second phase of divergences occurred by the uplift of the Central American isthmus, completed during the Pleistocene, resulting in the isolation and development of two cognates, *T. californica* and *T. gothica,* in the eastern Pacific.

The morphological divergence between these latter two species, which are sympatric over part of their ranges along the eastern Pacific, during the past million years can be indicative of the rate of speciation in *Thalamoporella.* Morphological differences in the type of spicules, the basal insertions, the shape and size of avicularia, even the rate of ovicell production, all point to a divergence process which may still be active. Interestingly, these two species are unique among the *T. gothica* complex in having four pore plates on each lateral zooidal wall. These unidirectional plates allow for the interzooidal connection of funicular tissues, which serve as a type of transport system within the colony. The other species of the complex possess only two plates on each lateral wall, although the plates have a relatively larger diameter. The morphological significance of differences in plate number is not yet understood but it serves as further indirect evidence that *T. gothica* is a sibling species recently diverged from *T. californica.*

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